

**DESICCATION SUSCEPTIBILITY OF THE DESERT  
BRACHYPTEROUS THIRIPS *ARPEDIOTHRIPS MOJAVE*  
HOOD (THYSANOPTERA: THIRIPIDAE)**

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*Abstract.*—Desiccation susceptibility of brachypterous *Arpediothrips mojave* Hood, a terebrantian thrips found on *Yucca* spp. between young leaves, was compared with that of *Frankliniella occidentalis* (Pergande), a widespread terebrantian thrips found on flowers. The longevity of adult female thrips withheld food and subjected to different vapor pressure deficits was measured. Across vapor pressure deficits, *A. mojave* survived 151 min, 0.28 times as long as *F. occidentalis* (545 min). Survival time decreased hyperbolically in *A. mojave* and linearly in *F. occidentalis* as vapor pressure deficit increased. The different trends indicate cuticular transpiration contributed more to desiccation in *A. mojave* than in *F. occidentalis*. Estimated surface-area to volume ratio of *A. mojave* was 2.1 times greater than *F. occidentalis*, primarily due to the former's flattened body. Survival time of *A. mojave* was 0.58 times as long as *F. occidentalis* after accounting for surface-area to volume ratio, suggesting greater cuticular permeability in *A. mojave*. Brachypterous *A. mojave* appear morphologically and physiologically restricted to their microhabitat between the leaves of *Yucca*.

*Key Words.*—Insecta, Thysanoptera, *Arpediothrips mojave*, *Yucca*, *Frankliniella occidentalis*, brachypterous, water loss.

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*Arpediothrips mojave* Hood is a terebrantian thrips of the Mojave Desert in California and Arizona (Bailey 1957). The species is found between the leaves of *Yucca* spp., where it feeds on soft tissue at the base of leaves. Bailey (1957) suggested *A. mojave* is restricted to *Yucca brevifolia* Englemann. Cott (1956), contrasting *A. mojave* with the tubuliferan thrips *Bagnalliella mojave* Hood, described the former as not limited to a single host and as especially abundant east of Charleston Peak in Clark County, Nevada. *Arpediothrips mojave* is polymorphic with brachypterous forms more common (Cott 1956). I have found aggregations of brachypterous *A. mojave* between young, appressed leaves of both *Y. brevifolia* and *Yucca schidigera* Roehl ex Ortgies (Fig. 1). *Yucca schidigera* grows on dry, rocky slopes throughout the Mojave Desert below 1500 m. This shrubby tree grows to 5 m in height and produces sharply-pointed leaves 30–60 cm long and 3–4 cm wide growing in rosettes atop single or branched trunks composed of dead leaves (Turner et al. 1995). *Yucca schidigera* photosynthesizes by crassulacean acid metabolism; transpiration is reduced by the stomates opening at night.

*Arpediothrips mojave*'s small size, brachyptery, and occurrence between leaves resembles characteristics of cryptozoic arthropods, animals that typically are small, wingless, hidden, and restricted to moist environments due to their permeable integuments and consequential rapid rates of desiccation (Cloudsley-Thompson 1988). Within Insecta, the cryptozoa are best represented by apterygote inhabitants of soil. This study examines *A. mojave*'s susceptibility to desiccation when removed from its between-leaf microhabitat. Desiccation susceptibility is compared with that of the ubiquitous thrips *Frankliniella occidentalis* (Pergande). *Frankliniella occidentalis*, western flower thrips, is the most common thrips in California and inhabits flowers of a diverse array of species, plant communities,

and climates (Bailey 1957). Its economic importance has made the species well-studied, including the effects of temperature and humidity on survival (Shipp & Gillespie 1993).

#### MATERIALS AND METHODS

*Arpediothrips mojave* were collected from *Y. schidigera* near Nelson, Clark County, Nevada. Thrips between young leaves at the center of a rosette were aspirated into a disposable pipette. The pipette was plugged with cotton and placed into an airtight container covered on the bottom with a wet cloth to saturate the container's air. *Frankliniella occidentalis* were collected by inserting ornamental roses harvested from my home (Boulder City, Clark County, Nevada) garden into a plastic bag. The two species were collected within 2 h of each other with *A. mojave* collected first in two trials and *F. occidentalis* collected first in two trials.

Survival time of the thrips was estimated with cages constructed of a brass washer (1 mm thick, 22 mm outside diameter, 10 mm hole diameter) smoothed on both sides with emory cloth and glued flat against a 30 mm × 30 mm piece of insect-labelling paper. The washer was covered on top with a 15 mm diameter round microscope cover glass loosely held in place by four beads of glue on the washer. Brachypterous adult female *A. mojave* or adult female *F. occidentalis* were selected without regard to size and placed into each cage by transferring them with a moistened brush onto the center of the cover glass laid on a cold plate under a microscope. After four thrips of the same species were transferred onto the cover glass, it was inverted and placed atop the washer.

Two cages each containing a different species were placed into a plastic food container with a clear top. The container also enclosed a digital hygrothermometer with an accuracy of  $\pm 5\%$  RH and  $\pm 1^\circ$  C (Extech Instruments, Waltham, Massachusetts). The cages and hygrothermometer were supported 10 mm above the container bottom to allow air flow underneath. A 5 mm diameter hole had been melted into two opposite sides of each container, and a 1.5 cm long plastic tube had been glued into one of the holes.

Five containers each enclosing both species in separate cages and a hygrothermometer were assembled. The containers were connected in series by inserting the plastic tube of one container into the hole of another and air, produced from aquarium pumps and saturated by bubbling through water, was passed through them. The initial time was recorded, and each container was disconnected and its holes sealed when the enclosed hygrothermometer displayed one of five relative humidities: 30%, 42%, 54%, 66%, or 78%. The number of surviving thrips, observed with a microscope through the container top and cage cover glass, and the relative humidity and temperature within the container were recorded every 30 min until all thrips were dead. Saturated air was added as needed to the containers individually to maintain the desired, displayed relative humidity  $\pm 2\%$  (room relative humidity was  $\leq 30\%$ ). Containers were kept at room temperature (25.7–30.0 [ $27.9 \pm 0.9$ ]° C).

Four trials, each composed of the five relative humidities tested concurrently, were performed on separate days (20, 22, 27, and 29 April 1999). The container and hygrothermometer used for each relative humidity were randomized within trials. The order of species placed within cages and cage location were randomized within containers. Vapor pressure deficit in kilopascals (kPa) within cages was

calculated from the average temperature and relative humidity in each container during each trial. Departure from normality (Kolmogorov-Smirnov/Lilliefors test,  $D = 0.15$ ,  $df = 158$ ,  $P < 0.001$ ; SPSS version 6.1, Chicago, Illinois) by the distribution of survival times was corrected ( $D = 0.07$ ,  $df = 158$ ,  $P = 0.052$ ) by transforming  $\ln(Y)$ . Thrips within the same cage were considered as subsamples (Neter et al. 1996) and their transformed survival times averaged. One thrips of each species, in the 66% RH ( $\approx 1.25$  kPa) treatment, died at the beginning of separate trials; two of the 40 cages therefore contained a subsample of three thrips and analyses were weighted accordingly.

Transformed survival times were analyzed by the general linear test approach (Neter et al. 1996). This approach compares one linear model against the same model but with fewer parameters. The omitted parameters contribute significantly to the model if their omission increases, as determined by an  $F$ -test, the error sum of squares. The error sum of squares for different linear models, starting with the full model, was calculated using multiple regression. The full model used transformed survival time as the dependent variable and species (spp), vapor pressure deficit (vpd), vapor pressure deficit squared ( $\text{vpd}^2$ ), and the cross-products between species and vapor pressure deficit ( $\text{spp} \times \text{vpd}$ ) and species and vapor pressure deficit squared ( $\text{spp} \times \text{vpd}^2$ ) as independent variables. Species were coded as an indicator variable (Neter et al. 1996). Interaction between species and vapor pressure deficit was tested by comparing the models (dependent variable and coefficients not shown): (1)  $\text{spp} + \text{vpd} + \text{vpd}^2 + (\text{spp} \times \text{vpd}) + (\text{spp} \times \text{vpd}^2)$ , and (2)  $\text{spp} + \text{vpd} + \text{vpd}^2$ . Species was tested by comparing: (1)  $\text{spp} + \text{vpd} + \text{vpd}^2$ , and (2)  $\text{vpd} + \text{vpd}^2$ . Vapor pressure deficit was tested by comparing: (1)  $\text{spp} + \text{vpd} + \text{vpd}^2$ , and (2)  $\text{spp}$ . Within each species, multiple regression was performed testing linear (vpd) and curvilinear ( $\text{vpd} + \text{vpd}^2$ ) trends across vapor pressure deficits. The curvilinear trend in *A. mojave* was more-accurately represented ( $r^2$  increased) by linearly regressing transformed survival time against vapor pressure deficit transformed  $1/X$ . Transforming  $1/X$  straightens hyperbolic curves (Sokal & Rohlf 1981). Resulting regression equations were used to fit lines to plotted data.

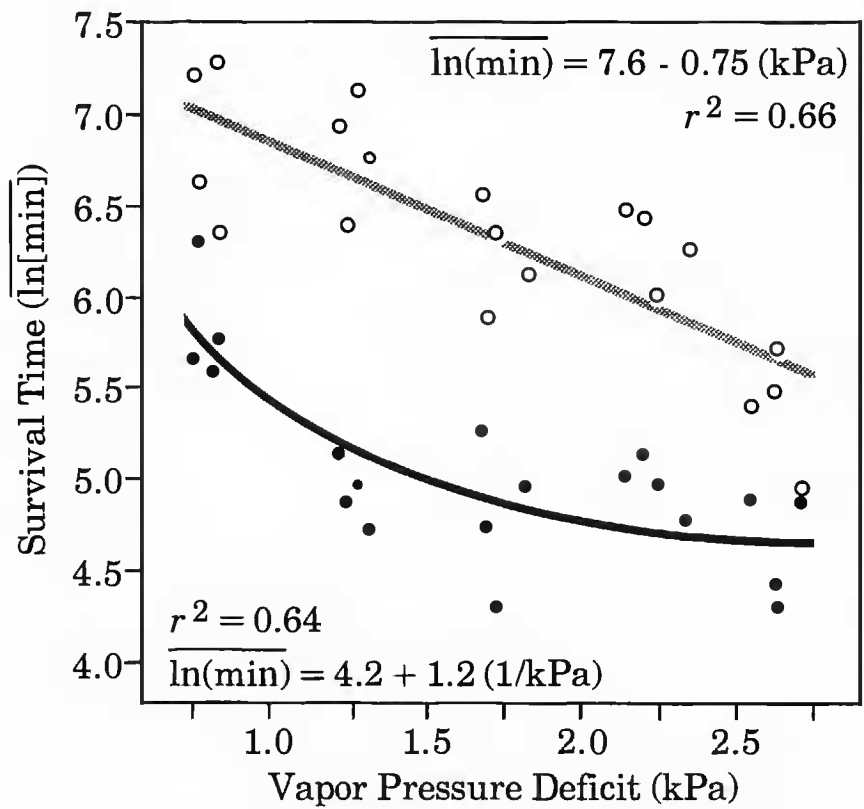
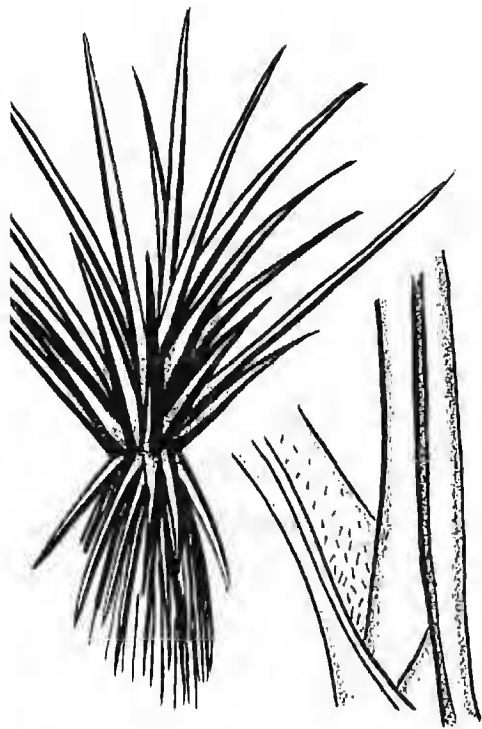
The potential influence of surface-area to volume ratio on survival time was examined by measuring ( $\pm 0.03$  mm) with an ocular micrometer at  $30\times$  the medial length ( $L$ ), maximum width ( $W$ ) of ventral aspect (left to right), and maximum height ( $H$ ) of lateral aspect (dorsum to ventrum, excluding wings on *F. occidentalis*) of adult females of each species ( $n = 22$ ). Thrips used for the measurements were collected 3 May 1999 and selected without regard to size. An elliptic cylinder was used as an approximation of overall body shape to calculate lateral (without cylinder ends) surface areas ( $S$ ), volumes ( $V$ ), and lateral surface-area to volume ratios for each individual with the formulas:

$$S = 2\pi L[(H^2 + W^2)/8]^{1/2}$$

$$V = \pi LHW/4$$

The contributions of wings and appendages to body surface-areas and volumes were discounted. Appendages expectedly would represent a small proportion of overall body surface area and volume, and the wings of *F. occidentalis* cover the dorsum, making their affect on water loss unclear.

Dimensions, surface areas, volumes, and surface-area to volume ratios were compared between species with  $t$ -tests. To determine if the difference in survival



Figures 1–2. Fig. 1. Rosette of *Yucca schidigera* leaves and depiction of brachypterous *Arpediothrips mojave* on the inner, concave surface of a separated appressed leaf. Fig. 2. Survival time of *Frankliniella occidentalis* (open circles) and *A. mojave* (closed circles) plotted against vapor pressure deficit. Each data point is the mean of four thrips, except smaller symbols (near 1.25 kPa) are the mean of three thrips. Equations and  $r^2$  values are for regressions performed separately for each species.

time between species was attributed to surface-area to volume ratio, survival times were multiplied by the species' surface-area to volume ratio and the general linear test of difference between species repeated. One of each species was slide mounted, verified as *A. mojave* or *F. occidentalis* (R. J. Gill, personal communication) and deposited at the University of California, Riverside, Entomology Museum.

## RESULTS

Transformed survival times (Fig. 2) differed between species ( $F = 115.4$ ;  $df = 1,36$ ;  $P < 0.001$ ) and decreased with increasing vapor pressure deficit ( $F = 24.4$ ;  $df = 2,36$ ;  $P < 0.001$ ). Across vapor pressure deficits, *F. occidentalis* adult females survived 545 min (retransformed mean) and brachypterous *A. mojave* adult females survived 151 min, 0.28 times as long. Species and vapor pressure deficit also interacted ( $F = 4.8$ ;  $df = 2,34$ ;  $P < 0.025$ ), indicating nonparallel rates of decrease in transformed survival time with increasing vapor pressure deficit. The full model explained 86% of the variation in transformed survival time. In *A. mojave*, a curvilinear decrease ( $r^2 = 0.61$ ) in transformed survival time across vapor pressure deficits was observed; both the linear (vpd;  $F = 8.5$ ;  $df = 1,17$ ;  $P = 0.01$ ) and quadratic (vpd<sup>2</sup>;  $F = 5.0$ ;  $df = 1,17$ ;  $P = 0.04$ ) terms were significant. Replacing the polynomial regression with a linear regression ( $F = 32.3$ ;  $df = 1,18$ ;  $P < 0.001$ ) against vapor pressure deficit transformed  $1/X$  improved the fit ( $r^2 = 0.64$ ). In *F. occidentalis*, transformed survival time decreased only linearly ( $F = 34.6$ ;  $df = 1,18$ ;  $P < 0.001$ ) across vapor pressure deficits; the quadratic term was not significant ( $F = 2.7$ ;  $df = 1,17$ ;  $P = 0.12$ ). Different trends, linear and hyperbolic, across vapor pressure deficits by the two



species agrees with the significant interaction detected by the general linear test approach.

Length, ventral width, and lateral height (mean  $\pm$  SD) were  $1.11 \pm 0.07$  mm,  $0.22 \pm 0.02$  mm, and  $0.08 \pm 0.02$  mm in *A. mojave* and  $1.25 \pm 0.10$  mm,  $0.26 \pm 0.02$  mm, and  $0.20 \pm 0.03$  mm in *F. occidentalis*. Lateral surface areas, volumes, and surface-area to volume ratios (mean  $\pm$  SD) were  $0.6 \pm 0.05$  mm<sup>2</sup>,  $0.02 \pm 0.004$  mm<sup>3</sup>, and  $38 \pm 6.7$  in *A. mojave* and  $0.9 \pm 0.2$  mm<sup>2</sup>,  $0.05 \pm 0.01$  mm<sup>3</sup>, and  $18 \pm 2.0$  in *F. occidentalis*. The two species differed (*A. mojave* smaller) in length ( $t = 5.19$ ;  $P < 0.001$ ), ventral width ( $t = 6.68$ ;  $P < 0.001$ ), lateral height ( $t = 16.1$ ;  $P < 0.001$ ), lateral surface area ( $t = 9.73$ ;  $P < 0.001$ ), and volume ( $t = 11.5$ ;  $P < 0.001$ ). Lateral surface-area to volume ratios also differed ( $t = 12.9$ ;  $P < 0.001$ ) between species, being 2.1 times greater in *A. mojave* compared with *F. occidentalis*. This difference primarily was due to the former's flattened body; *A. mojave*'s lateral height was 0.4 that of *F. occidentalis*. Adjusting for the species' surface-area to volume ratio did not eliminate the difference ( $F = 21.9$ ;  $df = 1,36$ ;  $P < 0.001$ ) in survival times between species across vapor pressure deficits. *Arpediothrips mojave* survived 0.58 times as long as *F. occidentalis* after accounting for surface-area to volume ratio.

#### DISCUSSION

Survival time of starved insects expectedly decreases hyperbolically with increasing vapor pressure deficit, assuming a linear increase in the rate of water loss with increasing vapor pressure deficit and death occurring when a constant amount of water has been lost (Bursell 1974). Cuticular transpiration (water loss per time) supports the first assumption; most water lost by insects is through the cuticle, and the rate of loss generally increases linearly as vapor pressure deficit increases (Hadley 1994). However, a linear rate of water loss via the cuticle may be obscured by water additionally lost from respiratory (spiracular) transpiration and excretion or gained from metabolism, resulting in longevities that deviate from the expected hyperbolic trend (Bursell 1974). Brachypterous *A. mojave* adult females exhibited a hyperbolic decrease in survival time, indicating cuticular transpiration as the dominant cause of desiccation. In contrast, the linear decrease in longevity of *F. occidentalis* adult females with increasing vapor pressure deficit suggests cuticular transpiration contributed a smaller proportion to the overall rate of desiccation.

Insect surface-area to volume ratio would have influenced desiccation rate and resulting survival time. Greater body volume would increase the thrips' water reserves and extend longevity. Greater body surface area would increase the total amount of water lost per time through the cuticle and shorten longevity. The 0.58 times shorter survival time by *A. mojave* compared with *F. occidentalis*, after accounting for surface-area to volume ratio, may have been due to greater ( $1/0.58 = 1.7$  times greater) cuticular permeability (water loss per cuticle surface area per time) by the former species. A more-permeable cuticle in *A. mojave* also is suggested by the species' fragility; specimens preserved in 70% ethanol are more translucent than *F. occidentalis* and often tear into fragments.

Antarctic Collembola, soil-inhabiting apterygote insects similar in size to the Thysanoptera studied here, provide a parallel association between desiccation rate and microhabitat (Block et al. 1990). *Parisotoma octooculata* (Willem), a spring-

tail restricted to damp soils, has a lower water content and higher rate of water loss compared with *Cryptopygus antarcticus* (Willem), a more abundant springtail found in soils with greater variation in soil moisture.

*Arpediothrips mojave* appears physiologically and morphologically adapted to its specialized habitat between the leaves of *Y. schidigera*. These adaptations are interrelated; the low vapor pressure deficit provided by *Y. schidigera*'s microhabitat allows the compressed body-plan, and increased surface-area to volume ratio, required by *A. mojave* to live between the appressed leaves. The flattened morphology also is enabled by brachyptery, frequently found in thrips inhabiting cramped locations (Lewis 1973). In addition, the ventral aspect of the head of *A. mojave* is unusually wide and long for a terebrantian, with the mouth cone extending almost to the posterior margin of the prosternum (Bailey 1957). The head therefore is flattened and stretched posteriad.

Reliance by brachypterous *A. mojave* on its moist and sparse microhabitat, surrounded by desert, requires macropterous forms to provide the species' dispersal. A shift from brachypterous to macropterous forms in *A. mojave* has been hypothesized to occur in response to unfavorable environmental conditions, such as plant water stress (Hood 1941, cited in Cott 1956). Further studies should examine the structure and function of macropterous *A. mojave* and their relation to brachypterous populations.

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